Running head: Hormones and body odour attractiveness

The scent of attractiveness: Levels of reproductive hormones explain individual differences in women's body odour

Janek S. Lobmaier[1], Urs Fischbacher[2,3], Urs Wirthmüller[4], Daria Knoch[1]

[1] Department of Social Psychology and Social Neuroscience, Institute of Psychology, University of Bern, Bern, Switzerland

[2] Department of Economics, University of Konstanz, Konstanz, Germany

[3] Thurgau Institute of Economics, Kreuzlingen, Switzerland

[4] Universitätsinstitut für Klinische Chemie, University of Bern, Bern, Switzerland

Authors for correspondence :
Janek Lobmaier : janek.lobmaier@psy.unibe.ch
Daria Knoch : daria.knoch@psy.unibe.ch

Abstract

Individuals are thought to have their own distinctive body odour which reportedly plays an important role in mate choice. In the present study we investigated individual differences in body odours of women and examined whether some women generally smell more attractive than others or whether odour preferences are a matter of individual taste. We then explored whether levels of reproductive hormones explain women's body odour attractiveness, to test the idea that body odour attractiveness may act as a chemosensory marker of reproductive fitness. Fifty-seven men rated body odours of 28 healthy, naturally cycling women of reproductive age. We collected all odours at peak fertility to control for menstrual cycle effects on body odour attractiveness. Women's salivary estradiol, progesterone, testosterone and cortisol levels were assessed at the time of odour collection to test whether hormone levels explain body odour attractiveness. We found that the men highly agreed on how attractive they found women's body odours. Interestingly, women's body odour attractiveness was predicted by their estradiol and progesterone levels: The higher a woman's levels of estradiol and the lower her levels of progesterone, the more attractive her body odour was rated. In showing that women's body odour attractiveness is explained by levels of female reproductive hormones, but not by levels of cortisol or testosterone, we provide evidence that body odour acts as a valid cue to potential fertility.

Keywords: olfaction, estradiol, progesterone, odour preference, human leucocyte antigen, HLA, major histocompatibility complex, MHC

1. Introduction

Olfaction allegedly plays an important role in mate choice of both human and non-human species [cf., 1, 2, 3]. It is widely thought that every individual has her own unique body odour, much like a fingerprint [4]. Here we collected women's body odours to examine whether some women generally smell more attractive than others or whether odour attractiveness lies "in the nose of the smeller". And if some women generally smell more attractive than others, can a woman's body odour attractiveness be explained by her individual levels of reproductive hormones (e.g., estradiol and progesterone)?

Studies on physical attractiveness of women's faces and bodies have found that men show remarkable agreement on who is seen as attractive and who not [e.g., 5, 6]. An evolutionary approach to female attractiveness proposes that men should generally prefer women who signal high reproductive health and fertility [e.g., 7, 8, 9]. In women, reproductive health can be indexed by levels of reproductive hormones: Elevated levels of female reproductive hormones increase the likelihood of conception [e.g., 10, 11]. Female reproductive hormones, in particular estradiol and progesterone, have been shown to be positively related to women's facial and body attractiveness. For example, higher levels of estradiol and progesterone lead to larger breasts and curvier waists, resulting in the hourglass figure that is typically preferred by men [12, 13; but see 14, 15]. Similarly, faces of women with higher estradiol levels are judged as being more attractive than faces of women with low estradiol levels [e.g., 16; but see 15, 17].

The present study investigates for the first time whether the same is true for women's body odours. Given that attractiveness is thought to signal various desirable qualities of a potential partner (e.g., health, reproductive success) and assuming that body odours play an important role in human mate choice [e.g., 2], it is likely that body odour attractiveness acts as a chemosensory signal of reproductive fitness. We hence expect individual levels in

reproductive hormones (e.g., estradiol and progesterone) to be related to women's body odour attractiveness.

Although no study has yet directly tested whether reproductive hormones are related to body odour attractiveness in women, there is some indirect evidence for a link between hormones and odour attractiveness. For example, in naturally cycling women body odour varies significantly across the menstrual cycle. An increasing number of studies report that women's body odour is rated as more attractive if gathered during the late follicular phase (near ovulation) compared to odour that was collected in other cycle phases [18-21]. The late follicular phase coincides with high estradiol and low progesterone levels. While within-woman variation in hormone levels may explain within-woman variance in body odour attractiveness, no study has yet directly investigated whether individual hormone levels are associated with between-women variation in body odour attractiveness.

The main source of human body odour are the apocrine sweat glands [cf. 22]. An individual's characteristic body odour results from various bacteria operating upon the viscous secretions of these glands, producing a complex mixture of volatile organic compounds [23-27]. Other candidates that contribute to body odour are odorous steroids and unsaturated fatty acids, such as 3M2H [e.g., 28]. Given that odorous steroids are related to reproductive hormones it is conceivable that levels of endogenous reproductive hormones are related to body odour. Men and women differ substantially in the structure and flora of the axillary scent glands [29-31] and in the odorous steroids contained in their sweat [32, 33]. These sex differences and the fact that they become active after puberty suggest that they play a role in sexual communication [34].

A further factor reported to influence body odour and body odour preferences are the genes at the major histocompatibility complex [MHC, or human leukocyte antigen system, HLA, in humans, see 35 for a review]. Some studies have suggested that men prefer body odours of HLA-dissimilar or HLA-heterozygous women [e.g., 36]. Studies looking at HLA-

mediated odour preferences imply that, rather than showing universal preferences for certain body odours, men have individual preferences for women's body odours, depending on the woman's and their own genetic make-up.

The present study sets out to investigate whether men agree when judging the attractiveness of women's body odours and if so, whether this can be explained by women's individual levels of reproductive hormones (estradiol, and progesterone). Because women's body odour has been reported to vary across the menstrual cycle [e.g., 18, 19], we controlled for cycle effects of body odour by collecting women's body odours during the late follicular phase (LH-peak). Hence, we not only controlled for menstrual cycle phase, but in fact also targeted odour collection to take place at peak fertility which, from a biological perspective, is the most relevant period of the menstrual cycle, since only then women can conceive. To control for HLA-associated odour preferences, we typed raters and donors at five HLA loci and calculated the HLA similarity between each rater and donor. We also calculated a measure of donor heterozygosity by adding up for each donor the number of alleles that were heterozygous. We collected axillary odour samples using cotton pads.

We first calculated the intraclass correlation coefficient (ICC) to quantify the inter-rater reliability. We then used multilevel linear regressions to test whether women's estradiol and progesterone levels predict the attractiveness of their body odour. Our analyses also considered potential effects of testosterone and HLA on body odour preferences. Levels of the stress hormone cortisol were also included, since stress and anxiety are known to have an impact on body odour [e.g., 37, 38]. The advantage of using multilevel regressions is that we can enter participants as level-2 variable with hormone levels and ratings nested within participants, enabling us to analyse the data without aggregating scores. Paralleling studies on facial and body attractiveness, we expect women's estradiol and progesterone levels to be positively associated with women's body odour attractiveness, since lifetime estradiol and progesterone are positively related to a woman's reproductive potential [e.g., 10, 12].

2. Methods

(a) Participants

Forty-two women (odour donors, mean age = 20.8, *SD* = 6.6) and 57 men (odour raters, mean age = 23, *SD* = 2.8) initially took part in this study. All participants reported being Caucasian and of European descent (at least back to their grandparents) and being heterosexual. The study was conducted according to the principles expressed in the Declaration of Helsinki. All participants provided written informed consent to take part in this study and were treated in accordance with the ethical protocol approved by the Faculty of Human Sciences of the University of Bern and by the Ethics Committee of the Canton of Bern. Odour donors received 140 CHF and odour raters received 45 CHF as compensation.

(b) Odour collection procedure

Odour donors (all female) were initially screened in a telephone interview for the required inclusion criteria: (a) aged between 17 and 40 years, (b) medication-free (including hormonal contraception for at least 3 previous months), (c) regular menstrual cycle (average length of between 25 and 35 days), (d) not pregnant or breastfeeding and (e) non-smoker. In the same telephone interview we also collected demographic information and information about their menstrual cycle (regularity, length and onset of last menstrual bleeding).

Using OvaCUE© fertility monitors, we predicted high fertility days during which odour collection was to take place (see electronic supplementary material, ESM1, Section A). One day before the date of predicted peak fertility, participants started collecting body odour using cotton axillary pads.

The odour donors were requested to follow a strict schedule of dietary and behavioural restrictions while collecting their body odour (see electronic supplementary material, ESM1 Section B, for details). On the evenings of the sampling, before applying the cotton axillary

pads to their left and right armpits, odour donors were instructed to take a shower with the non-perfumed soap supplied in the material package. Then donors fixed cotton pads (Ebelin cosmetic pads, DM-drogerie markt, www.dm-drogeriemarkt.de) to both armpits using 3M Micropore surgical tape. Donors collected body odour on three consecutive nights. To determine time of highest fertility, participants completed a series of urine tests measuring the luteinizing hormone (LH) using one-step urine ovulation tests with a reported LH sensitivity of 10mlU/ml (David One Step Ovulation Tests, Runbio Biotech, China, http://www.runbio-bio.com). Women were instructed to perform urine tests twice a day (morning and evening) starting one day before the date of predicted peak fertility. After a positive test result, participants continued performing the tests until the results became negative for two subsequent days. Participants photographed each test using their smart phones and sent the picture to the study manager, who verified whether the test was positive or not.

In the evenings before body odour collection, each donor collected a saliva sample from which steroid hormone levels (testosterone, estradiol, progesterone, and cortisol) were determined. Participants were instructed to refrain from eating and to abstain from caffeine for at least 30 minutes prior to saliva collection. Participants were asked to rinse their mouth with fresh water and to wait approximately 5 min before providing saliva. Samples were collected by passive drool using a commercially available sampling device (SaliCaps, IBL, International, Hamburg, Germany). The saliva samples were stored at -28°C and were later analyzed by an independent laboratory (Dresden Lab Service GmbH, Dresden, Germany) using liquid chromatography with coupled tandem mass spectrometry (LC-MS/MS). LC-MS/MS has become the method of choice for steroid analysis because of its high sensitivity, better reproducibility, greater specificity, and ability to analyse multiple steroids simultaneously.

After odour collection, the pads were stored in separate sealable plastic bags and were frozen at -30°C until use. Previous studies have shown that freezing has no significant effect on attractiveness ratings [39].

When returning their body odour samples to the lab, donors were asked a series of questions in a structured face-to-face interview, adapted from Gildersleeve and colleagues [40]. In this interview, we assessed how long the women had worn their axillary pads and whether they had complied with the dietary and behavioural restrictions (see electronic supplementary material, ESM1, Section C, for details).

(c) Donor dropouts

Only pads from the night closest to the LH peak were included in the study. Of the 42 women, nine did not show an LH peak during odour collection and five had violated the dietary and behavioural restrictions, resulting in a total of 28 donors who provided pads for the present study (age range: 18 - 36 years; mean = 26.9; SD= 3.6). We note that this range was rather skewed; there was only one woman who was 36, all the rest were between 18 and 28 years of age. Excluding the 36 year old woman from the analyses did not change the results (see electronic supplementary material, ESM3).

(d) Odour rating procedure

Every rater rated the body odours of all 28 women that were available for this study. Ratings took place on four afternoons. Each rater appeared on two of these afternoons, separated by one week. On each afternoon, raters evaluated the odours of 14 women. Half of the participants rated left-arm pads, the other half rated right-arm pads. Left and right arm pads were rated on separate afternoons. Each pad was hence defrosted only once for this study and was destroyed and disposed of after use. The pads were thawed three hours before the respective rating session started and were placed in separate 500ml opaque glass jars [cf. 41, 42, 43]. Three research assistants smelled the pads and confirmed that none was contaminated with extraneous odours (e.g., perfume, smoke).

To assess the odour preferences we closely followed the procedures reported in [41, 42]. To prepare for the rating session, odour raters (all male) were asked not to eat and to refrain from drinking caffeinated or alcoholic beverages for 1 h prior to testing, as these activities are known to affect smelling ability. After giving informed consent, the participants underwent two practice trials. Participants were asked to smell and rate the body odours of two women who were not included in the experiment proper. After the practice trials a male experimenter gave them a tube (SaliCaps, IBL, International, Hamburg, Germany) to collect their saliva sample from which we assessed testosterone levels. The saliva samples were stored at -28°C and were later analyzed together with the donors' saliva samples by an independent laboratory (Dresden Lab Service GmbH, Dresden, Germany) using LC-MS/MS.

In each session, odour raters rated the body odours of 14 different women. The jars containing the pads of these women were placed in separate visually shielded booths. Order of pads was randomized for each rater. Odour raters were asked to rate the women's body odour samples on a visual analogue scale (0-100) for attractiveness. If a rater found any of the samples too weak to assess, he was asked to select "I cannot smell the sample" instead of using the rating scales; these samples were not included in further analysis. Sniffing time was not restricted (see electronic supplementary material, ESM2, for details).

At the very end of the second session, participants were given 12 Sniffin' Sticks (Screening 12 Test, Burghart Messtechnik GmbH, www.burghart-mt.de), to evaluate their general smelling abilities.

All data collection was conducted using Qualtrics (www.qualtrics.com), running on individual portable tablet computers.

(e) Rater dropouts

One rater did not return for the second test session, and another scored low on the Sniffin' Sticks (score of 3 out of 12). These two raters were excluded from further analyses.

The final sample hence consisted of 55 raters ranging in age between 20 and 37 years (mean = 23; SD = 2.9). Of these, four did not provide blood samples for HLA analyses.

(f) HLA typing procedure

All participants (28 women, 57 men) were invited to the laboratory for venous blood sampling. Before blood sampling, participants read the study information and gave written informed consent. The participants' blood samples (10 ml) were genotyped for HLA-class I (HLA-A, HLA-B and HLA-C) and class II (HLA-DRB1, HLA-DQB1) using LinkSēq™ test kits (Linkage Biosystems™). These test kits are based on real-time polymerase chain reaction (PCR) using allele-specific exponential amplification (sequence-specific primers). The resulting amplimers were subjected at end-point to a melting curve analysis to identify specific DNA based on melting temperature using SYBR® Green. Attribution of HLA-genotypes was done using SureTyper™ software. Ambiguities were resolved using alternative typing methods via routine HLA-typing.

3. Statistical analysis

Statistical analyses were performed using SPSS 24.0 and level of significance was set at $p < .05$. We first calculated the intraclass correlation coefficient (ICC) to quantify how much the raters agree on the attractiveness of women's odours. We then ran multilevel linear regressions with attractiveness ratings as dependent variables. The first model included estradiol and progesterone levels as Level-1 predictors of body odour judgements. Raters were entered at Level 2. We then repeated the analysis after adding the estradiol x progesterone interaction as additional Level 1 predictor. In a second model, we included testosterone and cortisol together with estradiol and progesterone levels at Level 1. In a third model, we included rater testosterone levels together with donor estradiol and progesterone at Level 1 to examine whether testosterone influences body odour perception. This analysis was

repeated after adding the donor estradiol x rater testosterone and donor progesterone x rater testosterone interactions as additional Level 1 predictor. In a final model, we controlled for the influence of HLA similarity between raters and donors. To do so, we calculated an HLA-Similarity-Index for each rater-donor pair. We also calculated a continuous measure of HLA-heterozygosity by adding up for each donor the number of alleles that were heterozygous. These HLA indices were then entered as covariates, together with donor estradiol and progesterone levels.

The reported estimates in the multilevel models are unstandardised regression coefficients. Because examination of hormonal data revealed that the distributions were skewed, we log transformed the hormone values to achieve normal distributions. We report analyses performed with log-transformed data, but whether we used raw or normalised data did not change the results.

4. Results

A total of 1540 (28 x 55) ratings were completed. Of these, 101 (6.5 %) were rated as not perceivable. We note that the non-perceivable trials were not always from the same pad (i.e., woman). In other words, there was no pad that was not perceivable in all cases: the non-perceivable pads did not come from specific women, but were randomly distributed over different donors. Ratings of left and right pads correlated with $R = .668$, $p < .001$, and there was no significant difference between the attractiveness of left and right pads ($p = .886$), therefore they were pooled for all subsequent analyses.

Hormone data: For donors, estradiol levels ranged from 3.2 pg/ml to 15.6 pg/ml (mean = 7.1, *SD* = 3.1), progesterone levels ranged from 2.5 pg/ml to 87.7 pg/ml (mean = 21.3, SD = 22.0), testosterone levels ranged from 3.2 pg/ml to 15.8 pg/ml (mean = 7.7, *SD* = 3.5), and cortisol levels from 0.3 nmol/L to 10.6 nmol/L (mean = 2.1, *SD* = 2.3). For raters, we

286 measured only testosterone levels, ranging from 37.15 pg/ml to 118.3 pg/ml (mean = 70.02,
287 *SD* = 19.18).
288 *Interrater-reliability:* Intraclass correlation was high (ICC = .983), indicating excellent
289 reliability. This suggests that raters agreed highly on which odours they found more and
290 which ones they found less attractive.
291 *Body odour attractiveness:* The model including donor estradiol and progesterone levels
292 as covariates revealed that a woman's estradiol and progesterone levels both significantly
293 predicted her body odour attractiveness. For estradiol, the relationship was positive
294 (*Unstandardised Regression Coefficient (Estimate)* = 9.62; *standard error (SE)* = 3.225;
295 95%CI [3.29, 15.95]; t = 2.982, df = 1376.042; p = .003) and for progesterone the relationship
296 was negative (*Estimate* = -10.83; *SE* = 1.295; 95%CI [-13.371, -8.290]; t = -8.362; df =
297 1378.216; $p < .001$). The estradiol x progesterone interaction did not reach statistical
298 significance (*Estimate* = 10.52; *SE* = 6.809; 95%CI [-2.832, 23.880]; t = 1.546; df =
299 1375.512; p = .122). Figure 1 depicts the positive relationship between estradiol and body
300 odour attractiveness ratings (left panel) and the negative relationship between progesterone
301 and attractiveness ratings (right panel).
302 --- Figure 1 about here ---
303 When additionally entering donor testosterone and cortisol levels into the model, the
304 effects for estradiol (*Estimate* = 11.73; *SE* = 3.536; 95%CI [4.794, 18.667]; t = 3.318; df =
305 1374.949; p = .001) and progesterone (*Estimate* = -10.28; *SE* = 1.357; 95%CI [-12.938, -
306 7.614]; t = -7.573; df = 1375.700; $p < .001$) remained significant, the effects of testosterone
307 (*Estimate* = -.265; *SE* = 3.210; 95%CI [-6.562, 6.032]; t = -.083; df = 1374.558; p = .934) and
308 cortisol (*Estimate* = -2.040; *SE*=1.656; 95%CI [-5.288, 1.209]; t = -1.232; df = 1376.047; p =
309 .218) were not significant.
310 The third model, where we tested for influences of men's testosterone levels on their
311 ratings of women's body odour attractiveness, we again found effects of donor estradiol

(*Estimate* = 9.590; *SE* = 3.228; 95%CI [3.258, 15.921]; *t* = 2.971; *df* = 1374.445; *p* = .003) and progesterone (*Estimate* = -10.829; *SE* = 1.296; 95% CI [-13.371, -8.286]; *t* = -8.356; *df* = 1376.452; *p* < .001) but no effect of rater testosterone (*Estimate* = 4.272; *SE* = 5.025; 95%CI [-5.637, 14.180]; *t* = .850; *df* = 1199.656; *p* = .396). Also, neither the rater testosterone x donor estradiol interaction (*Estimate* = -21.425; *SE* = 21.531; 95%CI [-63.663, 20.812]; *t* = --.995; *df* = 1388.165; *p* = .320) nor the rater testosterone x donor progesterone interaction (*Estimate* = -12.056; *SE* = 8.361; 95%CI [-28.458, 4.347]; *t* = -1.442; *df* = 1376.426; *p* = .150) were significant.

The final model, where we additionally included HLA-similarity between donor and rater and donor HLA-heterozygosity as covariates, again showed significant effects of estradiol (*Estimate* = 8.634; *SE* = 3.421; 95%CI [1.921, 15.347]; *t* = 2.523; *df* = 1273.149; *p* = .012) and progesterone (*Estimate* = -11.027; *SE* = 1.347; 95%CI [-13.669, -8.385]; *t* = -8.189; *df* = 1275.034; *p* < .001), but no effect of HLA similarity (*Estimate* = .34; *SE* = 0.351; 95%CI [-.344, 1.034]; *t* = .983; *df* = 1323.910; *p* = .326) or HLA heterozygosity (*Estimate* = 64.65; *SE* = .434; 95%CI [-1.494, .209]; *t* = 1.480; *df* = 1275.174; *p* = .139).

5. Discussion

We tested whether women's individual levels of reproductive hormones (e.g., estradiol and progesterone) are associated with how attractive they smell and to what extent men agree when judging the attractiveness of different women's body odours. We found that men highly agreed on which odours they found attractive and which ones they liked less. Most interestingly, we found that women's levels of endogenous estradiol and progesterone predicted their body odour attractiveness. Specifically, women's body odours were rated as being more attractive the higher their estradiol levels and the lower their progesterone levels were. Cortisol and testosterone levels were not associated with how attractive women's body odours were rated.

From an evolutionary point of view female attractiveness is thought to provide cues to various desirable qualities that males may seek for in mates. Having high estradiol levels is one of the desirable traits that men may seek in a woman, since estradiol is positively related to a woman's reproductive potential [e.g., 10]. Hence, selection on preferences for cues potentially signalling high estradiol levels is likely to be strong, because they provide information about a woman's future, or potential, fertility [11, 44]. The present study provides evidence that estradiol is positively related to women's body odour attractiveness, suggesting that body odour acts as a reliable cue to potential fertility.

Interestingly, we found a negative relation between women's progesterone levels and their body odour attractiveness. This may seem surprising because lifetime progesterone levels are thought to be positively related to a woman's reproductive potential [e.g., 10, 12]. We note however that we collected all body odours at peak fertility, when women naturally smell their best [cf., 18, 19, 21, 40]. At peak fertility, women typically have high estradiol and low progesterone levels, and the estradiol-to-progesterone ratio is highly correlated with women's fertility across the menstrual cycle [45, 46]. Even though all the odour samples in the present study came from currently fertile women, raters chose those odours to be most attractive that came from women who were most fertile at that moment (i.e., who had highest estradiol levels and lowest progesterone levels). This supports the notion that body odour is a cue to fertility: the higher a woman's fertility, the more attractive her body odour was to men.

The biochemical mechanism underlying the relationship between sex steroids and women's body odour is not clear. One possibility is that sex hormones act indirectly on body odour via body temperature regulation. It has been shown that the control of skin blood flow and sweating are modified by estradiol and progesterone, whereby estradiol promotes heat dissipation (i.e., augmented cutaneous vasodilation and higher propensity of sweating, [47]) and progesterone is reported to promote heat conservation [for reviews see 48, 49]. Increased skin blood flow and sweating may lead to the excretion of certain odorous volatiles which on

their part might function as a cue to higher estradiol levels. A more direct explanation for the effect of hormones on body odour might be that the axillary region secrets odorous compounds resembling estradiol and progesterone. Transferred to our findings, this means that an attractive body odour is a particularly female odour. Alternatively, estradiol and progesterone may act directly on the volatile compounds or on the bacteria operating upon the viscous secretions of various sweat glands. These hypotheses, while speculative in nature, may help explain the interrelation between levels of female sex steroids and body odour attractiveness, but will have to be specifically tested in future studies.

Because some studies have found that body odour preferences are mediated by the human leukocyte antigen, [HLA, see 35 for a review] we controlled for HLA-mediated effects of body odour preferences by including HLA-similarity between donor and rater at five HLA loci and donor HLA-heterozygosity as covariates. Neither of these genetic measures predicted woman's body odour attractiveness. These results add to the growing body of literature that questions HLA-mediated odour preferences in men [e.g., 42, 50, 51; for a meta-analysis, see 52].

Together our findings suggest that some women generally smell nicer than others and that the attractiveness of women's body odour is influenced by their estradiol and progesterone levels rather than by individual preferences of the rater or by human leucocyte antigens (HLA). Chemical communication of sex and reproductive stage are ubiquitous in the animal kingdom, facilitating sexual selection that arises through competition over mates [53]. Our results provide strong evidence that humans also use chemical signals to communicate their reproductive potential. Since estradiol and progesterone levels can be seen as indices of reproductive health and fertility, we propose that body odours serve as reliable cues to women's reproductive fitness.

Ethics

The study was approved by the Ethics Committees of the Faculty of Human Sciences of the University of Bern (Nr.: 2016-11-00004) and of the Canton of Bern (KEK-Nr.: 242/ 15) and was conducted according to the principles expressed in the Declaration of Helsinki.

Data accessibility

The dataset used for this manuscript is available at datadryad.org.

https://doi.org/10.5061/dryad.g5n1785

Author contributions

JL, UF & DK designed the study, UW performed HLA typing, JL & UF analysed the data, JL & DK wrote the manuscript, UF und UW provided helpful input on manuscript drafts.

Competing interests

All authors gave final approval for publication and have no competing interests.

Acknowledgements

We thank Nicole Ruffieux, Susanne Kanzler, Peggy Kübler and Fabian Probst for their organizational support, Amira Bösch and Flavio Schmidig for their assistance in recruiting and testing participants, and Sandra Augsburger, Andrea Odermatt and Annalea Klainguti for HLA-typing. We are grateful for helpful discussions with Martin Müller and Alexandra Kohl Schwarz.

Funding

This work was supported by a grant from the Typhaine Foundation awarded to DK and a grant from the Swiss National Science Foundation awarded to JSL (grant number PP00P1_163758/1).

References:

1. Roberts S.C., Gosling L.M., Carter V., Petrie M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. *Proc Biol Sci* **275**(1652), 2715-2722. (doi:F542428772R96X64 [pii] 10.1098/rspb.2008.0825).
2. Lubke K.T., Pause B.M. 2015 Always follow your nose: The functional significance of social chemosignals in human reproduction and survival. *Hormones and Behavior* **68**, 134-144. (doi:10.1016/j.yhbeh.2014.10.001).
3. Gosling L.M., Roberts S.C. 2001 Scent-marking by male mammals: Cheat-proof signals to competitors and mates. *Adv Stud Behav* **30**, 169-217. (doi:Doi 10.1016/S0065-3454(01)80007-3).
4. Penn D.J., Oberzaucher E., Grammer K., Fischer G., Soini H.A., Wiesler D., Novotny M.V., Dixon S.J., Xu Y., Brereton R.G. 2007 Individual and gender fingerprints in human body odour. *J R Soc Interface* **4**(13), 331-340. (doi:C14291T735824274 [pii] 10.1098/rsif.2006.0182).
5. Langlois J.H., Kalakanis L., Rubenstein A.J., Larson A., Hallam M., Smoot M. 2000 Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological Bulletin* **126**(3), 390-423. (doi:10.1037/0033-2909.126.3.390).
6. Cunningham M.R., Roberts A.R., Wu C.H., Barbee A.P., Druen P.B. 1995 Their Ideas of Beauty Are, on the Whole, the Same as Ours - Consistency and Variability in the Cross-Cultural Perception of Female Physical Attractiveness. *Journal of Personality and Social Psychology* **68**(2), 261-279. (doi:Doi 10.1037//0022-3514.68.2.261).
7. Symons D. 1979 *The evolution of human sexuality*. Oxford, Oxford University Press.
8. Thornhill R., Grammer K. 1999 The body and face of woman: One ornament that signals quality? *Evolution and Human Behavior* **20**(2), 105-120. (doi:10.1016/s1090-5138(98)00044-0).
9. Thornhill R., Gangestad S.W. 1999 Facial attractiveness. *Trends Cogn Sci* **3**(12), 452-460. (doi:S1364-6613(99)01403-5 [pii]).
10. Jasienska G. 2013 *The fragile wisdom: an evolutionary view on women's biology and health*. Cambridge MA, Harvard University Press.
11. Lipson S.F., Ellison P.T. 1996 Comparison of salivary steroid profiles in naturally occurring conception and non-conception cycles. *Hum Reprod* **11**(10), 2090-2096.
12. Jasienska G., Ziomkiewicz A., Ellison P.T., Lipson S.F., Thune I. 2004 Large breasts and narrow waists indicate high reproductive potential in women. *Proceedings of the Royal Society B-Biological Sciences* **271**(1545), 1213-1217. (doi:10.1098/rspb.2004.2712).

13. Singh D. 1993 Adaptive Significance of Female Physical Attractiveness - Role of Waist-to-Hip Ratio. *Journal of Personality and Social Psychology* **65**(2), 293-307. (doi:Doi 10.1037/0022-3514.65.2.293).
14. Grillot R.L., Simmons Z.L., Lukaszewski A.W., Roney J.R. 2014 Hormonal and morphological predictors of women's body attractiveness. *Evolution and Human Behavior* **35**(3), 176-183.
15. Jones B.C., Hahn A.C., Fisher C.I., Wang H., Kandrik M., Lao J., Han C., Lee A.J., Holzleitner I.J., DeBruine L.M. 2018 No compelling evidence that more physically attractive young adult women have higher estradiol or progesterone. *bioRxiv*. (doi:10.1101/136515).
16. Law Smith M.J., Perrett D.I., Jones B.C., Cornwell R.E., Moore F.R., Feinberg D.R., Boothroyd L.G., Durrani S.J., Stirrat M.R., Whiten S., et al. 2006 Facial appearance is a cue to oestrogen levels in women. *Proceedings of the Royal Society B-Biological Sciences* **273**(1583), 135-140. (doi:10.1098/rspb.2005.3296).
17. Puts D.A., Bailey D.H., Cardenas R.A., Burriss R.P., Welling L.L.M., Wheatley J.R., Dawood K. 2013 Women's attractiveness changes with estradiol and progesterone across the ovulatory cycle. *Hormones and Behavior* **63**(1), 13-19. (doi:10.1016/j.yhbeh.2012.11.007).
18. Singh D., Bronstad P.M. 2001 Female body odour is a potential cue to ovulation. *Proceedings of the Royal Society B* **268**, 797-801.
19. Gildersleeve K.A., Haselton M.G., Larson C.M., Pillsworth E.G. 2012 Body odor attractiveness as a cue of impending ovulation in women: evidence from a study using hormone-confirmed ovulation. *Horm Behav* **61**(2), 157-166. (doi:10.1016/j.yhbeh.2011.11.005).
20. Havlicek J., Dvorakova R., Bartos L., Flegr J. 2006 Non-advertised does not mean concealed: Body odour changes across the human mestrual cycle. *Ethology* **112**, 81-90.
21. Cerda-Molina A.L., Hernandez-Lopez L., de la O C.E., Chavira-Ramirez R., Mondragon-Ceballos R. 2013 Changes in Men's Salivary Testosterone and Cortisol Levels, and in Sexual Desire after Smelling Female Axillary and Vulvar Scents. *Frontiers in endocrinology* **4**, 159. (doi:10.3389/fendo.2013.00159).
22. Doty R.L. 1981 Olfactory Communication in Humans. *Chem Senses* **6**(4), 351-376. (doi:DOI 10.1093/chemse/6.4.351).
23. Albone E.S., Gosden P.E., Ware G.C., Macdonald D.W., Hough N. 1977 Bacterial Action and Chemical Signaling in Red Fox and Other Mammals. *Abstr Pap Am Chem S* **174**(Sep), 22-22.
24. Leyden J.J., McGinley K.J., Holzle E., Labows J.N., Kligman A.M. 1981 The microbiology of the human axilla and its relationship to axillary odor. *J Invest Dermatol* **77**(5), 413-416.
25. Stoddart D.M. 1990 *The scented ape: the biology and culture of human odor*. Cambridge, UK, Cambridge University Press.
26. Taylor D., Daulby A., Grimshaw S., James G., Mercer J., Vaziri S. 2003 Characterization of the microflora of the human axilla. *Int J Cosmet Sci* **25**(3), 137-145. (doi:10.1046/j.1467-2494.2003.00181.x).
27. James A.G., Hyliands D., Johnston H. 2004 Generation of volatile fatty acids by axillary bacteria. *Int J Cosmet Sci* **26**(3), 149-156. (doi:10.1111/j.1467-2494.2004.00214.x).
28. Martin A., Saathoff M., Kuhn F., Max H., Terstegen L., Natsch A. 2010 A functional ABCC11 allele is essential in the biochemical formation of human axillary odor. *J Invest Dermatol* **130**(2), 529-540. (doi:10.1038/jid.2009.254).

29. Doty R.L., Orndorff M.M., Leyden J., Kligman A. 1978 Communication of gender from human axillary odors: relationship to perceived intensity and hedonicity. *Behav Biol* **23**(3), 373-380.
30. Jackman P.J., Noble W.C. 1983 Normal axillary skin microflora in various populations. *Clin Exp Dermatol* **8**(3), 259-268.
31. Brody B. 1975 The sexual significance of the axillae. *Psychiatry* **38**(3), 278-289.
32. Gower D.B., Ruparelia B.A. 1993 Olfaction in humans with special reference to odorous 16-androstenes: their occurrence, perception and possible social, psychological and sexual impact. *J Endocrinol* **137**(2), 167-187.
33. Gower D.B., Bird S., Sharma P., House F.R. 1985 Axillary 5 alpha-androst-16-en-3-one in men and women: relationships with olfactory acuity to odorous 16-androstenes. *Experientia* **41**(9), 1134-1136.
34. Hays W.S.T. 2003 Human pheromones: have they been demonstrated? *Behav Ecol Sociobiol* **54**(2), 89-97. (doi:10.1007/s00265-003-0613-4).
35. Havlicek J., Roberts S.C. 2009 MHC-correlated mate choice in humans: a review. *Psychoneuroendocrinology* **34**(4), 497-512. (doi:S0306-4530(08)00266-7 [pii] 10.1016/j.psyneuen.2008.10.007).
36. Thornhill R., Gangestad S.W., Miller R., Scheyd G., McCollough J.K., Franklin M. 2003 Major histocompatibility complex genes, symmetry, and body scent attractiveness in men and women. *Behavioral Ecology* **14**(5), 668-678. (doi:10.1093/beheco/arg043).
37. Prehn A., Ohrt A., Sojka B., Ferstl R., Pause B.M. 2006 Chemosensory anxiety signals augment the startle reflex in humans. *Neuroscience Letters* **394**(2), 127-130. (doi:10.1016/j.neulet.2005.10.012).
38. Mujica-Parodi L.R., Strey H.H., Frederick B., Savoy R., Cox D., Botanov Y., Tolkunov D., Rubin D., Weber J. 2009 Chemosensory Cues to Conspecific Emotional Stress Activate Amygdala in Humans. *Plos One* **4**(7). (doi:ARTN e6415 10.1371/journal.pone.0006415).
39. Lenochova P., Roberts S.C., Havlicek J. 2009 Methods of Human Body Odor Sampling: The Effect of Freezing. *Chem Senses* **34**(2), 127-138. (doi:10.1093/chemse/bjn067).
40. Gildersleeve K.A., Fales M.R., Haselton M.G. 2017 Women's evaluations of other women's natural body odor depend on target's fertility status. *Evol Hum Behav* **38**(2), 155-163.
41. Roberts S.C., Gosling L.M., Carter V., Petrie M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. *Proceedings of the Royal Society B-Biological Sciences* **275**(1652), 2715-2722. (doi:10.1098/rspb.2008.0825).
42. Probst F., Fischbacher U., Lobmaier J.S., Wirthmuller U., Knoch D. 2017 Men's preferences for women's body odours are not associated with human leucocyte antigen. *Proc Biol Sci* **284**(1864). (doi:10.1098/rspb.2017.1830).
43. Fialova J., Roberts S.C., Havlicek J. 2016 Consumption of garlic positively affects hedonic perception of axillary body odour. *Appetite* **97**, 8-15. (doi:10.1016/j.appet.2015.11.001).
44. Venners S.A., Liu X., Perry M.J., Korrick S.A., Li Z., Yang F., Yang J., Lasley B.L., Xu X., Wang X. 2006 Urinary estrogen and progesterone metabolite concentrations in menstrual cycles of fertile women with non-conception, early pregnancy loss or clinical pregnancy. *Hum Reprod* **21**(9), 2272-2280. (doi:10.1093/humrep/del187).
45. Landgren B.M., Unden A.L., Diczfalusy E. 1980 Hormonal profile of the cycle in 68 normally menstruating women. *Acta Endocrinol (Copenh)* **94**(1), 89-98.

46. Baird D.D., Weinberg C.R., Wilcox A.J., McConnaughey D.R., Musey P.I. 1991 Using the ratio of urinary oestrogen and progesterone metabolites to estimate day of ovulation. *Stat Med* **10**(2), 255-266.
47. Stephenson L.A., Kolka M.A. 1999 Esophageal temperature threshold for sweating decreases before ovulation in premenopausal women. *J Appl Physiol (1985)* **86**(1), 22-28. (doi:10.1152/jappl.1999.86.1.22).
48. Charkoudian N., Hart E.C.J., Barnes J.N., Joyner M.J. 2017 Autonomic control of body temperature and blood pressure: influences of female sex hormones. *Clin Auton Res* **27**(3), 149-155. (doi:10.1007/s10286-017-0420-z).
49. Charkoudian N., Stachenfeld N. 2016 Sex hormone effects on autonomic mechanisms of thermoregulation in humans. *Auton Neurosci* **196**, 75-80. (doi:10.1016/j.autneu.2015.11.004).
50. Kromer J., Hummel T., Pietrowski D., Giani A.S., Sauter J., Ehninger G., Schmidt A.H., Croy I. 2016 Influence of HLA on human partnership and sexual satisfaction. *Scientific Reports* **6**, 32550. (doi:10.1038/srep32550).
51. Santos P.S.C., Schinemann J.A., Gabardo J., Bicalho M.D. 2005 New evidence that the MHC influences odor perception in humans: a study with 58 Southern Brazilian students. *Hormones and Behavior* **47**(4), 384-388. (doi:10.1016/j.yhbeh.2004.11.005).
52. Winternitz J., Abbate J.L., Huchard E., Havlicek J., Garamszegi L.Z. 2017 Patterns of MHC-dependent mate selection in humans and nonhuman primates: a meta-analysis. *Mol Ecol* **26**(2), 668-688. (doi:10.1111/mec.13920).
53. Wyatt T.D. 2003 *Pheromones and animal behavior: communication by smell and taste*. London, Cambridge University Press.

Figure Captions:

Figure 1. Relationship between mean odour attractiveness ratings and estradiol levels (left panel) and progesterone levels (right panel), including regression lines and confidence intervals (95%).